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Non-methane biogenic volatile organic compound emissions from boreal peatland microcosms under warming and water table drawdown

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Abstract Boreal peatlands have significant emissions of non-methane biogenic volatile organic compounds (BVOCs). Climate warming is expected to affect these ecosystems both directly, with increasing temperature, and indirectly, through water table drawdown following increased evapotranspiration. We assessed the combined effect of warming and water table drawdown on the BVOC emissions from boreal peatland microcosms. We also assessed the treatment effects on the BVOC emissions from the peat soil after the 7-week long experiment. Emissions of isoprene, monoterpenes, sesquiterpenes, other reactive VOCs and other VOCs were sampled using a conventional chamber technique, collected on adsorbent and analyzed by GC–MS. Carbon emitted as BVOCs was less than 1% of the CO_2 uptake and up to 3% of CH_4 emission. Water table drawdown surpassed the direct warming effect and significantly decreased the emissions of all BVOC groups. Only isoprene emission was significantly increased by warming, parallel to the increased leaf number of the dominant sedge *Eriophorum vaginatum*. BVOC emissions from peat soil were higher under the control and warming treatments than water table drawdown, suggesting an increased activity of anaerobic microbial community. Our results suggest that boreal peatlands could have concomitant negative and positive radiative forcing effects on climate warming following the effect of water table drawdown. The observed decrease in CH_4 emission causes a negative radiative forcing while the increase in CO_2 emission and decrease in reactive BVOC emissions, which could reduce the cooling effect induced by the lower formation rate of secondary organic aerosols, both contribute to increased radiative forcing.

Keywords Isoprene · Monoterpene · Sesquiterpene · BVOC · Climate warming · Bog

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Introduction

Boreal and subarctic peatlands cover a territory of approx. 350 million ha globally and act as important carbon sinks (Gorham 1991). These ecosystems release also significant amount of non-methane biogenic volatile organic compounds (BVOCs) in the atmosphere (Klinger et al. 1994; Tiiva et al. 2007a; Bäckstrand et al. 2008; Faubert et al. 2010b).

Several studies have concentrated on the effect of climate warming on carbon dioxide (CO_2) and methane (CH_4) exchanges from boreal peatlands (Strack 2008) but more studies on BVOC emissions are needed.

Plants release BVOCs under optimal conditions as well as in reaction to mild and severe physiological or mechanical stresses (Laothawornkitkul et al. 2009; Niinemets 2010). BVOCs are of high importance in the atmospheric chemistry where their reactions with oxides of nitrogen form tropospheric ozone (Chameides et al. 1988; Laothawornkitkul et al. 2009; Peñuelas and Staudt 2010). BVOCs also compete with CH_4 for OH radicals, which lengthens the lifetime of CH_4 in the atmosphere (Kaplan et al. 2006). The BVOC oxidation cycle in the atmosphere forms secondary organic aerosols and its end product is CO_2 (Fehsenfeld et al. 1992; Fuentes et al. 2000; Peñuelas and Staudt 2010). Therefore, BVOC emissions affect the atmospheric concentrations of the three major greenhouse gases (ozone, CH_4 and CO_2) but the role of BVOCs in the formation of secondary organic aerosols has a cooling effect (IPCC 2007). However, the interactions between BVOC emissions, greenhouse gases and secondary organic aerosols have unknown feedbacks on climate warming (IPCC 2007; Peñuelas and Staudt 2010).

Climate warming has a direct effect on the boreal peatland ecosystem as elevated air temperature affects ecological and biogeochemical processes (Strack 2008). Elevated temperature increases instantaneous emissions of isoprene, monoterpenes and sesquiterpenes, as well as the emission capacity of leaves (i.e. the emission at standard temperature and photosynthetic photon flux density—PPFD—values; Monson et al. 1992; Guenther et al. 1995; Sharkey et al. 1999; Pétron et al. 2001; Duhl et al. 2008). Moreover, it was recently reported that climate warming increases the isoprene emission by 56–83% and doubles the monoterpene and sesquiterpene emissions from subarctic tundra (Tiiva et al. 2008; Faubert et al. 2010a). Therefore, we need to know if such a drastic increase of BVOC emissions would also occur in boreal peatlands.

Boreal peatlands are also indirectly affected by climate warming that is responsible for water table drawdown following an increase in ecosystem evapotranspiration (IPCC 2007). Water table drawdown and water stress related to drought decrease BVOC emissions in the cases of severe stress (Sharkey and Loreto 1993; Bertin and Staudt 1996; Pegoraro et al. 2004; Brilli et al. 2007; Lavoir et al. 2009; Niinemets 2010; Peñuelas and Staudt 2010), whereas mild water stress increases or does not affect the emissions (Staudt et al. 2008; Niinemets 2010; Peñuelas and Staudt 2010). After the relief of a severe water stress, BVOC emissions have been reported to be higher than the pre-stress level (Sharkey and Loreto 1993; Brilli et al. 2007; Niinemets 2010; Peñuelas and Staudt 2010). Furthermore, BVOC emissions are coupled with carbon uptake in conditions of water stress (Bertin and Staudt 1996; Brilli et al. 2007; Lavoir et al. 2009). In a boreal Scots pine forest, drought increased BVOC emissions (Lappalainen et al. 2009), whereas in boreal peatlands water table drawdown decreased the emissions of isoprene, monoterpenes and other less reactive BVOCs (Tiiva et al. 2009; Faubert et al. 2010c). BVOC emissions from soil can be released from microbial processes depending on the aerobic conditions (Asensio et al. 2007; Insam and Seewald 2010; Seewald et al. 2010). In boreal peatland soil, water table controls the oxicity (Strack 2008) and this has potential impacts on BVOC emissions.

To summarize, in the ecosystems studied so far, warming and water table drawdown have antagonistic effects on BVOC emissions; emissions are increased by warming (Tiiva et al. 2008; Faubert et al. 2010a) and decreased by water table drawdown (Tiiva et al. 2009; Faubert et al. 2010c). Our aims in this study were to assess the effect of warming and water table drawdown, both alone and in concert, on the BVOC emissions from boreal peatland microcosms. We predicted that the direct effect of warming would increase the emissions of isoprene, monoterpenes and sesquiterpenes according to their temperature dependency (Monson et al. 1992; Guenther et al. 1995; Duhl et al. 2008) and the increase of these emissions under warming recently reported on a subarctic heath (Tiiva et al. 2008; Faubert et al. 2010a). The water table drawdown was predicted to decrease emissions of all BVOC groups as reported in another microcosm experiment (Tiiva et al. 2009; Faubert et al. 2010c). BVOC emissions from the peat layer in the microcosms were also measured at the end of the 7-week long experiment to determine if warming and water table treatments could have also affected BVOC release from the soil. The proportion of

carbon emitted as BVOCs was determined relative to the net ecosystem CO_2 and CH_4 exchanges in order to investigate the relationship between the carbon emitted as BVOCs and the total carbon exchange.

Materials and methods

Collection of peatland microcosms and conditions in growth chambers

The microcosms were collected on 25 August 2008 from the lawn microtopography of an ombrotrophic peatland, Turvesuo peatland, in Suonenjoki, Central Finland (62°40′ N, 26°58′ E, 102 m a.s.l.). Microcosms (depth 40 cm, diameter 10.5 cm) were cored directly into PVC tubes plugged at the bottom using an adapted peat corer (Tiiva et al. 2009; Faubert et al. 2010c). The lawn vegetation was dominated by a *Sphagnum* spp. moss cover, the sedge *Eriophorum vaginatum* L. and the dwarf shrub *Andromeda polifolia* L. (Table 1). The vegetation biomass at the end of the experiment is presented in detail in Table 1. The leaves of *E. vaginatum* were counted every week of the experiment.

After the collection, the microcosms rested outdoors under shade for 12 days and were watered with water collected from the peatland. On 5 September 2008, the microcosms were transferred to the growth chambers (Weiss Bio 1300, Weiss Umwelttechnik Gmbh, Reiskirchen-Lindenstruth, Germany). Microcosms were watered daily in the growth chambers using first the peatland water until the stock ended and then distilled water was used. Microcosms with water table at the surface were watered up to the surface, whereas those with water table drawdown were watered up to 20 cm depth, that is, up to four holes drilled at 20 cm depth from the top. The conditions in the growth chambers were set to the mean weather of July in central Finland and followed the average variation during a cycle of a 24-h day (Temperature 15.0–22.4°C, humidity 64–96%, light/dark cycle 20 h/4 h, maximum PPFD received by vegetation 450 μmol m^{-2} s^{-1}). The growth chambers containing the microcosms under the warming treatment were set to an air temperature of 5°C superior to the mean in July. This increased soil temperature at 5–20 cm depth by approx. 4.2°C. These growth conditions were maintained for 7 weeks.

Experimental design

The full factorial randomized experimental design consisted of 36 microcosms placed in six growth chambers. Three growth chambers were set to the mean air temperature of July in central Finland and another three to an air temperature 5°C superior to the

Table 1 Mean (±SE; $n = 3$) aboveground dry biomass (g m^{-2}) of plant species harvested at 2 cm depth after the 7-week long experiment on boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT)

Type of biomass	Species	C	WT	T	T + WT
Vascular plants	*Andromeda polifolia*	23.7 (10.9)	8.7 (3.5)	17.1 (8.1)	17.9 (4.0)
	Betula nana	<0.1	0.3 (0.1)	<0.1	0.3 (0.2)
	Carex spp.	3.6 (1.8)	4.2 (1.8)	3.9 (2.4)	3.1 (1.6)
	Drosera rotundifolia	0.2 (0.1)	0.1 (0.1)	4 (3.4)	0.3 (0.2)
	Eriophorum vaginatum	3.6 (1.6)	9.4 (3.7)	14.3 (7.3)	15.2 (4.9)
	Pinus sylvestris	0	0	0.6 (0.4)	0
	Vaccinium oxycoccos	12.5 (2.8)	10.3 (3.3)	11.1 (3.6)	13.7 (2.4)
	Total	43.5 (13.4)	33.1 (7.8)	51.0 (13.5)	50.4 (8.1)
Mosses	*Mylia anomala*	1.8 (0.5)	2.3 (1.2)	2.7 (1.3)	3.1 (1.6)
	Sphagnum spp.	386.8 (39.6)	410.7 (40.7)	412.2 (37.7)	385.5 (36.6)
	Warnstorfia fluitans	0	0	< 0.1	0.3 (0.3)
	Total	388.5 (39.6)	413.1 (40.5)	414.8 (37.9)	388.9 (36.5)
Lichen	*Cladopodiella fluitans*	0.3 (0.3)	<0.1	2.5 (1.5)	<0.1

mean of July ($n = 3$). There were six microcosms per growth chamber, of which three had water table at the surface and three had a water table drawn down by 20 cm done with holes drilled in the PVC tubes at 20 cm depth from the top. From here on, the microcosms in the mean temperature of July and water table at the surface are named "C" for control and those with water table drawdown are named "WT" (for the water table treatment). The microcosms in the warming treatment and water table at the surface are named "T" (for temperature) and those in the combined treatment are named "T + WT".

BVOC sampling

BVOC emissions were sampled six times during the experiment, approx. once a week, starting six days after the transfer of the microcosms in the growth chambers. The sampling technique was a conventional push–pull system used for measuring BVOC emissions from the whole plant/soil system (Tholl et al. 2006; Ortega and Helmig 2008; Tiiva et al. 2009; Faubert et al. 2010c). A transparent polycarbonate chamber (thickness 1.5 mm, diameter 13 cm, height 30 cm; Vink Finland, Kerava, Finland) was used to sample the air. The chamber was placed on a plastic collar fixed around the top of the microcosm during the measurements. Water was poured into the groove of the collar to seal the chamber headspace. The air sample for BVOC collection was pulled out through an Automatic Thermal Desorption (ATD) steel tube (Perkin Elmer, Boston, MA, USA) with a small battery-operated pump (12 V Rietschle Thomas, Puchheim, Germany). The ATD tube was filled with a combination of Tenax TA and Carbopack B adsorbents (100 mg of each, mesh 60/80, Supelco, Bellefonte, PA, USA).

The duration of the air sampling for BVOC collection was 30 min, during which air volume of 6 l was sampled. The outflow was set to 200 ml min^{-1} through the sample tube with a flow meter (Agilent Flow Tracker 1000, Agilent Technologies Inc., Wilmington, DE, USA). In order to prevent the entry of air from outside into the chamber, a slightly higher inflow was maintained by pumping air at a rate of 215 ml min^{-1} (Staudt et al. 2000; Tiiva et al. 2009). A purification system consisting of a charcoal filter and a MnO_2 scrubber was used to remove the BVOCs and ozone from the inflow air, respectively (Ortega and Helmig 2008). Thus, the BVOC concentrations in the inflow air were considered to be negligible thanks to the purification system. During the sampling period, the chamber air was circulated with a small fan. The mean air temperature (Tinyview Plus, Gemini Data Loggers Ltd., Chichester, UK) in the chamber headspace was 25.2 ± 0.1°C for control and WT microcosms and 30.3 ± 0.1°C for T and T + WT microcosms. The mean PPFD (quantum sensor LI-COR, Lincoln, NE, USA), was 293.2 ± 4.7 μmol m^{-2} s^{-1}. The adsorbent tubes were sealed with Teflon coated brass caps immediately after the sampling and kept refrigerated until the analysis (max. 18 days).

At the end of the experiment, the peat layer at the depth of 2–10 cm below the moss surface in each microcosm was sampled for BVOCs using the same method as in Tiiva et al. (2009) and Faubert et al. (2010c). Briefly, the peat samples were put in 1-l glass jars covered with an opaque cloth to ensure dark conditions. Air samples were collected from the glass jars at 21°C with a flow rate of 200 ml min^{-1} through the ATD tubes described earlier. The glass jars were flushed with charcoal filtered and MnO_2 scrubbed air through Teflon tubing at a flow rate of 220 ml min^{-1} during the 60-min sampling period. After the sampling, the peat was oven-dried at 60°C for 48 h and the emissions were proportioned to the peat dry weight.

BVOC analysis

The samples were analyzed by gas chromatography-mass spectrometry (Hewlett Packard 6890, MSD 5973, Palo Alto, CA, USA) after thermodesorption at 250°C and cryofocusing at −30°C with an automated thermal desorber (ATD400, Perkin Elmer, Wellesley, MA, USA). BVOCs were separated using a HP-5 capillary column (50 m × 0.2 mm, film thickness 0.33 μm). The carrier gas was helium. The oven temperature was held at 40°C for 1 min, then raised to 210°C at a rate of 5°C min^{-1}, and finally further to 250°C at a rate of 20°C min^{-1}.

BVOCs were identified according to the mass spectra in the Wiley data library, and quantified by pure standard compounds (Fluka, Buchs, Switzerland) according to total ion counts as in Faubert et al. (2010a). The compounds were classified into five groups: isoprene, monoterpenes, sesquiterpenes, other reactive volatile organic compounds (ORVOCs,

compounds with a lifetime of <1 day due to the reactions with the OH radicals, NO_3 and O_3; Guenther et al. 1995) and other volatile organic compounds (other VOCs, compounds with a lifetime >1 day; Guenther et al. 1995).

The chromatograms were analyzed using the Enhanced ChemStation software (G1701CA Version C.00.00 21 December 1999; Agilent Technologies, Santa Clara, CA, USA) followed by extracting and sorting the information by an in-house function. The dataset included the compounds that appeared in at least 10% of the measurements and had an identification quality (in Wiley data library) of above 90% (Faubert et al. 2010a).

The emission rates were calculated using the formula:

$$\frac{\text{BVOC mass in ATD tube [µg]}}{(\text{Sampling time of 30 [min]} \times \text{ Air flow through ATD tube 0.2 [L min}^{-1}])} \times \frac{\text{Chamber volume [L]}}{\text{Plot surface area [m}^2\text{]}} \times 2$$

where the BVOC mass in the ATD tube is divided by the air flow rate and sampling time, and then multiplied by the chamber volume to obtain the absolute amount of BVOCs in the headspace (Tiiva et al. 2009; Faubert et al. 2010a, c). The soil surface microtopography was taken into account when determining the chamber headspace volume (on average 3.7 l). The emission rate of BVOCs was finally divided by the surface area of the plot and multiplied by two to give the emission rate per hour.

Measurements of CO_2 and CH_4 effluxes

The CO_2 and CH_4 effluxes were measured during the weeks 3, 4, 6 and 7 of the experiment following the method in Niemi et al. (2002) and Tiiva et al. (2009). The net ecosystem CO_2 exchange (NEE) was determined by measuring the CO_2 concentration in the chamber headspace at 15-s interval for a maximum of 4 min using an infrared gas analyzer (LI 6262, LI-COR, Lincoln, NE). The mean air temperature in the ventilated transparent chamber during the NEE measurements was 24.7 ± 0.2°C for C and WT microcosms and 28.3 ± 0.2°C for T and T + WT microcosms; the mean PPFD was 318.2 ± 5.6 µmol m^{-2} s^{-1}. The dark ecosystem respiration (R_{TOT}), that is, peat and plant respiration, was also measured after NEE measurements using an opaque chamber with mean air temperature of 24.6 ± 0.2°C for C and WT microcosms and 28.4 ± 0.1°C for T and T + WT microcosms. The NEE and R_{TOT} were calculated from the linear change in the CO_2 concentration in the chamber headspace as a function of time, surface area, chamber volume and the molar volume of CO_2 at chamber air temperature. Positive values of NEE expressed a net CO_2 emission. The gross photosynthesis (P_G) was calculated by subtracting NEE to R_{TOT} ($P_G = R_{TOT} - NEE$; P_G and R_{TOT} expressed as positive values).

The CH_4 efflux was measured with four air samples of 60-ml taken into syringes from the headspace of a ventilated aluminum chamber at 3-min intervals. Air sampled for CH_4 measurement was replaced by an equal amount of ambient air to avoid negative pressure in the chamber headspace. The mean air temperature during air sampling for CH_4 was 24.9 ± 0.2°C for C and WT microcosms and 29.7 ± 0.1°C for T and T + WT microcosms. The air samples were analyzed for CH_4 using a gas chromatograph (HP 5890 Series II, Hewlett-Packard, Wilmington, DE) with a Haye-Sep Q column (80/100 mesh; length 1.8 m), and a flame ionisation detector (FID; Nykänen et al. 1995). The CH_4 efflux rate was calculated from the linear change in CH_4 concentration as a function of time, surface area, chamber volume and the molar volume of CH_4 at chamber air temperature. A small number of measurements were rejected from the data set due to bubbling during the sampling procedure.

Statistical analyses

The effect of warming and water table drawdown on the quantified BVOC emissions and the number of

E. vaginatum leaves in repeated measurements was tested using the linear mixed model procedure of the SPSS package 14.0 for Windows (SPSS Inc., Chicago, IL, USA). The model included warming, water table drawdown and time as fixed factors and the growth chamber as a random factor, with the factor time taking the repeated measurements on the same experimental units into account. The interactions between the fixed factors were kept in the model with P-value < 0.15. If warming or water table drawdown had a significant effect in the analysis done on the repeated measurements, linear mixed models were run separately on the measurement weeks to locate when the treatment had a significant effect. The growth chamber represented the unit of replication ($n = 3$).

Principal component analysis (PCA) was performed on the peak areas of the BVOC emissions using the SIMCA-P software version 11.5 (Umetrics, Umeå, Sweden) to assess how the treatments affected the BVOC emission profiles, that is, the relative amount of the different compounds emitted, and how the emissions were associated to each other to characterize the treatment effect. PCAs were done on the repeated measurements of the weekly BVOC emissions as well as on the emissions released by the peat layer at 2–10 cm at the end of the experiment. Outliers were removed and the principal components (PC) were extracted for each model after a unit variance scaling of the variables. The scores of each PC generated by the PCAs were then analyzed for treatment effects by the linear mixed model procedure in SPSS as described above.

Results

Effect of warming and water table drawdown on BVOC emissions

A total of 28 compounds were emitted from the boreal peatland microcosms during the experiment (isoprene, 10 monoterpenes, 4 sesquiterpenes, 11 ORVOCs, 2 other VOCs; Fig. 1, Electronic Supplementary Table S1). Warming significantly increased the isoprene emission by 280% whereas it did not significantly affect the emissions of other BVOC groups (Fig. 1). Isoprene emission was first

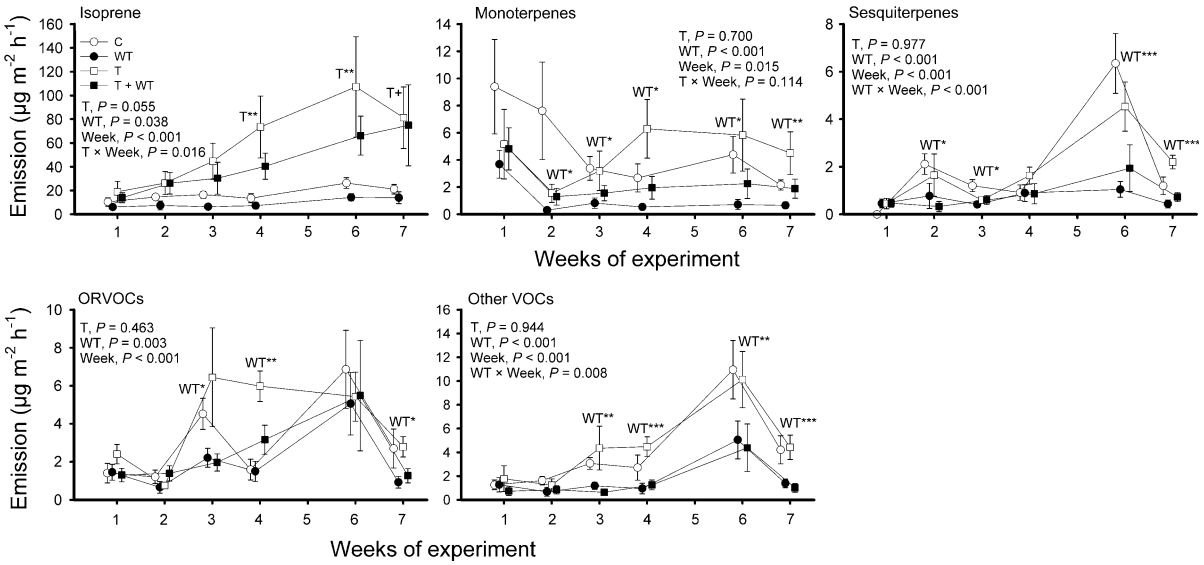

Fig. 1 The mean (± SE, $n = 2$–3) emissions of isoprene, monoterpenes, sesquiterpenes, other reactive volatile organic compounds (ORVOCs) and other volatile organic compounds (other VOCs) from boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT) during the 7-week long experiment. Note the different Y-axis scales. The P-values included in the linear mixed model analysis with warming, water table and time as fixed factors and growth chamber as a random factor are presented for each compound group. *Plus sign* and one, two and three *asterisks* signify treatment effects at $P < 0.1$, $P < 0.05$, $P < 0.01$ and $P < 0.001$ within a week, respectively

significantly increased by warming in the fourth week and it remained significantly higher than under normal temperature for the rest of the experiment.

Emissions of all BVOC groups, including isoprene, were significantly decreased by water table drawdown (Fig. 1). Isoprene, monoterpene, sesquiterpene, ORVOC and other VOC emissions were 50, 160, 160, 61 and 162% higher in the C and T than WT and T + WT microcosms for the whole experiment, respectively. Water table drawdown significantly decreased monoterpene and sesquiterpene emissions starting in the second week and this was maintained for the rest of the experiment, except for the sesquiterpenes in the fourth week (Fig. 1). ORVOC and other VOC emissions were significantly decreased by water table drawdown starting in the third week and this was maintained until the end of the experiment, except for the ORVOCs in the sixth week (Fig. 1).

The PCA revealed that water table drawdown significantly changed the BVOC emission mixture in the boreal peatland microcosms (Fig. 2). The C and T microcosms, with natural water table, were associated with relatively higher emissions of several monoterpenes: β-phellandrene, α-pinene, sabinene, β-myrcene, camphene, p-mentha-1(7),8-diene and limonene. Moreover, the emissions of these monoterpenes associated with natural water table positively correlated with each other (Fig. 2; Pearson correlation factors > 0.24; $P < 0.001$; $n = 209$–214) except for β-phellandrene and sabinene. The effect of water table treatment was significant on the scores of PCs 1 and 2 ($P < 0.001$), while temperature had no significant effects ($P > 0.38$; Fig. 2).

E. vaginatum: warming and water table drawdown effect, and correlations with BVOC emissions

The effect of warming on the number of *E. vaginatum* leaves was nearly significant during the whole experiment (Fig. 3). When the weeks were analyzed separately, warming significantly increased the number of *E. vaginatum* leaves from the fourth week onwards, as also observed for isoprene emission (Figs. 1, 3). On the other hand, water table drawdown did not affect the number of *E. vaginatum* leaves during the whole experiment.

In the microcosms under warming treatment (that is, T and T + WT), the number of *E. vaginatum* leaves correlated positively with the emissions of isoprene (Pearson correlation coefficient = 0.663, $P < 0.001$, $n = 108$), monoterpenes (Pearson correlation coefficient = 0.489, $P < 0.001$, $n = 106$) and ORVOCs (Pearson correlation coefficient = 0.248, $P = 0.010$, $n = 108$). In contrast, in the microcosms

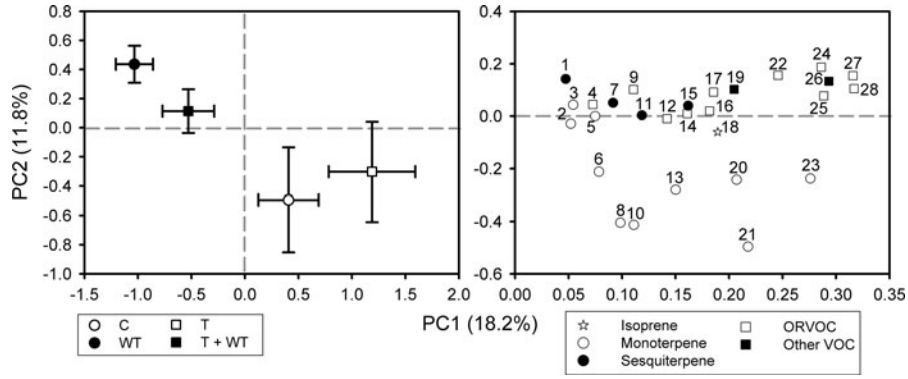

Fig. 2 Principal component analysis on the biogenic volatile organic compound (BVOC) emission profiles in boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT). The mean scores (±SE; $n = 18$) of the principal components (PC) for the 7-week long experiment are presented with the loading variables. The variation explained by each PC is in *parentheses*. Compound names: (*1*) 1,4-dimethyl-7-(prop-1-en-2-yl)-1,2,3,3a,4,5,6,7-octahydroazulene, (*2*) β-ocimene, (*3*) pin-2(3)-ene, (*4*) 1,3,5-trimethylbenzene, (*5*) 3-carene, (*6*) β-phellandrene, (*7*) alloaromadendrene, (*8*) camphene, (*9*) 2-heptene, (*10*) p-mentha-1(7),8-diene, (*11*) aromadendrene, (*12*) styrene, (*13*) α-pinene, (*14*) hexadecane, (*15*) δ-cadinene, (*16*) methyl-2-ethylhexanoate, (*17*) 3-xylene, (*18*) isoprene, (*19*) benzene, (*20*) sabinene, (*21*) limonene, (*22*) 4-xylene, (*23*) β-myrcene, (*24*) ethylbenzene, (*25*) 1,2,4-trimethylbenzene, (*26*) toluene, (*27*) 1,2,3-trimethylbenzene, (*28*) 3-ethyltoluene

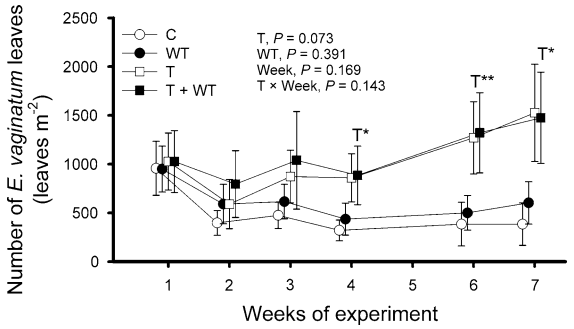

Fig. 3 The mean (±SE; $n = 3$) weekly number of *Eriophorum vaginatum* leaves in boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT) during the 7-week long experiment. The *P*-values included in the linear mixed model analysis with warming, water table and time as fixed factors and growth chamber as a random factor are presented. One and two *asterisks* signify treatment effects at $P < 0.05$ and $P < 0.01$ within a week, respectively

under normal temperature (that is, C and WT) sesquiterpene emissions alone correlated negatively with the number of *E. vaginatum* leaves (Pearson correlation coefficient $= -0.272$, $P = 0.005$, $n = 106$).

Peat BVOC emissions

A total amount of 83 compounds were released from the peat samples taken from the 2–10 cm depth in the boreal peatland microcosms (20 monoterpenes, 25 sesquiterpenes, 34 ORVOCs, 4 other VOCs; Fig. 4, Electronic Supplementary Table S2). The mean peat other VOC emissions were highest with 84.1 ± 32.7 (SE) ng g^{-1} (peat DW) h^{-1} averaged across all treatments, followed by monoterpenes, ORVOCs and sesquiterpenes with 47.9 ± 17.6, 17.9 ± 7.4 and 9.0 ± 2.6 ng g^{-1} (peat DW) h^{-1}, respectively. The PCA revealed that the treatments formed three associations of emissions: (1) C microcosms, (2) T microcosms and (3) WT and T + WT microcosms (Fig. 4; PC1, *P*-values from linear mixed model analysis: $P_{\text{Temperature}} = 0.370$, $P_{\text{Water table}} = 0.002$, $P_{\text{Temperature} \times \text{Water table}} = 0.030$; PC2, *P*-values: $P_{\text{Temperature}} = 0.955$, $P_{\text{Water table}} = 0.001$). The significant Temperature × Water table interaction appeared because both T and WT had lower scores on PC1 than C, but the scores of the combined treatment were between T and WT microcosms (Fig. 4).

Some monoterpenes (e.g. *p*-mentha-1(7),8-diene, α-terpinolene, camphor, 3-pinanone), several sesquiterpenes (δ-elemene, α-copene, α-gurjunene, β-caryophyllene, isoledene, β-maalinene, δ-cadinene, 1*s*,*cis*-calamenene and α-muurolene), some ORVOCs (e.g. dimethyldisulphide, *p*-Menth-8-ene, 3-menthene and dimethyltetrasulphide) and one other VOC (e.g. *tert*-butylbenzene) were associated with C microcosms, that is, with relatively higher emission rates under control than other treatments (Fig. 4, Electronic Supplementary Table S2). The T microcosms were associated with ORVOC emissions (e.g. 2-heptanone, 2-octanone, 2-nonanone and vitispirane; Fig. 4, Electronic Supplementary Table S2). The emission of one ORVOC (1-heptene) was associated with WT and T + WT microcosms (Fig. 4, Electronic Supplementary Table S2).

CO_2 and CH_4 exchanges and their relation with BVOC emissions

Warming and water table treatments affected significantly the CO_2 and CH_4 exchanges in the boreal peatland microcosms (Table 2). In WT and T + WT microcosms, water table drawdown induced a significant CO_2 emission while there was a CO_2 uptake in C and T microcosms with natural water table. Water table drawdown significantly decreased P_G while it significantly increased R_{TOT}. Moreover, R_{TOT} was significantly increased by warming in T and T + WT microcosms. CH_4 emission turned into CH_4 oxidation under water table drawdown in WT and T + WT microcosms. In T and T + WT microcosms, warming significantly increased CH_4 emission and decreased the oxidation. Water table drawdown significantly affected the total carbon exchange (that is, the sum of total BVOC–C, CO_2–C and CH_4–C exchanges) as there was a significant carbon uptake in C and T microcosms and carbon emission in WT and T + WT microcosms.

The BVOC–C emissions were 0.2 and 0.7% of the CO_2–C uptake in C and T microcosms, respectively (Table 2). In WT and T + WT microcosms, the BVOC–C emissions were 0.02 and 0.05% of the CO_2–C emission, respectively. For the CH_4 exchanges, the BVOC-C emissions were 2.9 and 1.5% of the CH_4–C emission in C and T microcosms, respectively. The BVOC–C emissions in WT and

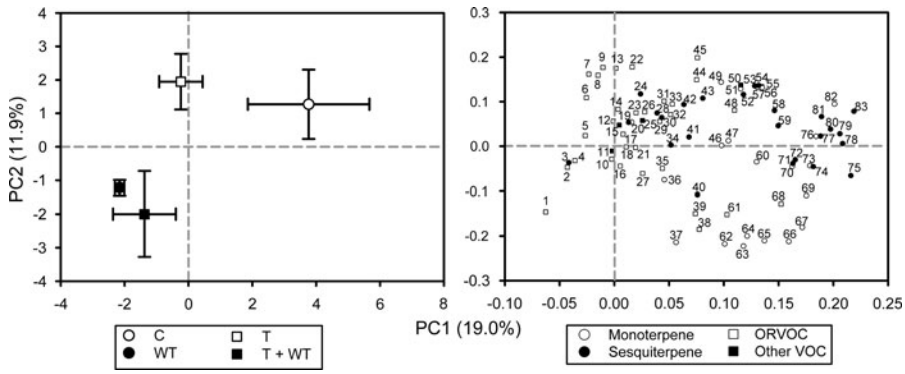

Fig. 4 Principal component analysis on the biogenic volatile organic compound (BVOC) emission profiles from the peat layer sampled at 2–10 cm depth after the 7-week experiment in boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT). The mean scores (±SE; $n = 3$) of the principal components (PC) are presented with the loading variables. The variation explained by each PC is in *parentheses*. Compound names: (*1*) 1-heptene, (*2*) 6(z),9(e)-heptadecadiene, (*3*) longifolene, (*4*) 4-methylcyclohexene, (*5*) 3-xylene, (*6*) styrene, (*7*) 2-octanone, (*8*) vitispirane, (*9*) 2-heptanone, (*10*) 1-heptadecene, (*11*) hexane, (*12*) 2-xylene, (*13*) 2-nonanone, (*14*) hexadecane, (*15*) toluene, (*16*) 3-methylpentane, (*17*) 2-methylpentane, (*18*) camphane, (*19*) β-selinene, (*20*) α-thujone, (*21*) 1,3-octadiene, (*22*) 2-undecanone, (*23*) 4-xylene, (*24*) 1,4-dimethyl-7-(prop-1-en-2-yl)-1,2,3,3a,4,5,6,7-octahydroazulene, (*25*) benzene, (*26*) 2-pentylfuran, (*27*) tridecane, (*28*) ylangene, (*29*) 1,2,3-trimethylbenzene, (*30*) α-calacorene, (*31*) 4-methyl-2-pentanone, (*32*) heptadecane, (*33*) 4-methyldecane, (*34*) β-cubebene, (*35*) 1,13-tetradecadiene, (*36*) sabinene, (*37*) pin-2(3)-ene, (*38*) 1-methyl-2-isopropylbenzene, (*39*) β-cymene, (*40*) longipinene, (*41*) ledene, (*42*) β-bourbonene, (*43*) valencene, (*44*) dimethyldisulfide, (*45*) dimethyltetrasulphide, (*46*) fenchyl alcohol, (*47*) γ-pyronene, (*48*) octane, (*49*) 3-pinanone, (*50*) *tert*-butylbenzene, (*51*) *p*-mentha-1(7),8-diene, (*52*) α-gurjunene, (*53*) 1*s*,*cis*-calamenene, (*54*) isoledene, (*55*) *p*-menth-8-ene, (*56*) camphor, (*57*) 3-menthene, (*58*) β-caryophyllene, (*59*) γ-caryophyllene, (*60*) fenchone, (*61*) 1-octene, (*62*) 3-carene, (*63*) tricyclene, (*64*) β-phellandrene, (*65*) α-pinene, (*66*) β-myrcene, (*67*) limonene, (*68*) verbenene, (*69*) γ-terpinene, (*70*) bicyclo[2.2.1]hept-2-ene,2,7,7-trimethyl, (*71*) β-guaiene, (*72*) epizonarene, (*73*) camphene, (*74*) aromadendrene, (*75*) germacrene-d, (*76*) α-fenchene, (*77*) γ-cadinene, (*78*) α-muurolene, (*79*) β-maaliene, (*80*) δ-cadinene, (*81*) δ-elemene, (*82*) α-terpinolene, (*83*) α-copaene

T + WT microcosms were 1.5 and 14.4% of the CH_4–C oxidation, respectively.

Discussion

Decreased BVOC emissions under water table drawdown

Water table drawdown decreased the emissions of all BVOC groups, as predicted. Water stress is known to reduce isoprene emission by plants (Sharkey and Loreto 1993; Pegoraro et al. 2004) and this result has also been reported in another experiment using boreal peatland microcosms (Tiiva et al. 2009). Water table drawdown could have also decreased isoprene emission through aerobic microbial degradation of isoprene in the peat (Cleveland and Yavitt 1998). Monoterpene emissions were also decreased by water table drawdown as measured in another experiment using boreal peatland microcosms (Faubert et al. 2010c). Additionally, emissions of several monoterpenes were associated to natural water table and positively correlated with each other. A reduction of monoterpene emissions has also been measured for Mediterranean species experiencing water stress caused by drought (Bertin and Staudt 1996; Llusià et al. 2006; Lavoir et al. 2009). Water table drawdown maintained for seven weeks in the present study could have been severe enough to cause a water stress to the vegetation, thus explaining the decreased BVOC emissions.

The decreases of monoterpene, sesquiterpene, ORVOC and other VOC emissions with water table drawdown could also have been induced by degradation processes occurring in the peat. The peat BVOC sampling done at the end of the experiment showed that several BVOCs of all groups were associated with the natural water table in the control and warming treatments while only one compound, 1-heptene, was associated with water table drawdown. This suggests that the anaerobic conditions in

Table 2 Mean (±SE; $n = 12$) emission of biogenic volatile organic compounds (BVOCs), net ecosystem CO_2 exchange (NEE) and CH_4 exchange in boreal peatland microcosms under control (C), water table drawdown (WT), warming (T) and combined treatments (T + WT) during weeks 3, 4, 6 and 7 of the experiment

	C	WT	T	T + WT	Statistical significance
Total BVOCs (mg BVOC–C m^{-2} h^{-1})	32.7 (3.0) × 10^{-3}	14.9 (2.6) × 10^{-3}	78.6 (22.2) × 10^{-3}	49.3 (9.2) × 10^{-3}	WT^{+}, Week*
NEE[a] (mg CO_2–C m^{-2} h^{-1})	−19.1 (2.8)	80.7 (6.3)	−11.3 (5.1)	97.4 (12.3)	WT***
P_G[b] (mg CO_2–C m^{-2} h^{-1})	50.9 (4.0)	22.7 (4.0)	79.8 (10.7)	42.4 (8.0)	WT***, Week^{+}
R_{TOT}[c] (mg CO_2–C m^{-2} h^{-1})	31.8 (3.2)	103.4 (6.3)	68.5 (9.2)	139.8 (12.0)	T***, WT***
CH_4[d] exchange (mg CH_4–C m^{-2} h^{-1})	1.1 (0.5)	−1.0 (0.5)	5.2 (1.9)	−0.3 (1.0)	T*, WT***
Total carbon exchange[e] (mg C m^{-2} h^{-1})	−17.9 (2.9)	79.7 (6.1)	−4.1 (4.8)	97.1 (12.3)	WT***

$^{+}$, * The statistical significances for the main effect of temperature (T) and water table (WT) treatments and time (Week) are presented at $^{+}$ $P < 0.1$, * $P < 0.05$ and *** $P < 0.001$ (linear mixed model analysis with T, WT and Week as fixed and growth chamber as random factors)

[a] NEE: Net ecosystem CO_2 exchange, positive values express a net CO_2 emission

[b] P_G: gross photosynthesis

[c] R_{TOT}: dark ecosystem respiration

[d] Positive values express a net CH_4 emission

[e] Total carbon exchange = Total BVOC + NEE + CH_4 exchange; positive values express a net carbon emission

the microcosms with natural water table may have increased the BVOC emissions released from the activity of anaerobic bacteria (Seewald et al. 2010). Moreover, warming combined with the anaerobic conditions may have increased the enzymatic activity of some anaerobic bacteria, causing a distinctive BVOC signature. In the microcosms with water table drawdown, it appears that BVOC uptake occurred in the increased oxic layer where aerobic conditions could have favored degradation of multiple BVOCs by microbial activity (Asensio et al. 2007; Insam and Seewald 2010).

Increased isoprene emission under warming

Warming increased isoprene emission from the boreal peatland microcosms, as predicted. This is also in line with the temperature dependency of isoprene emission (Monson et al. 1992) and the isoprene emission capacity of leaves that increases when growth is under elevated temperature (Sharkey et al. 1999; Pétron et al. 2001). Warming also increased the number of isoprene-emitting *E. vaginatum* leaves that indirectly increased isoprene emission (Tiiva et al. 2007b, 2009).

Apart from isoprene, warming did not increase the emissions of the other BVOC groups. This is contrary to our prediction and the usual temperature dependency of monoterpene and sesquiterpene emissions (Guenther et al. 1995; Duhl et al. 2008). However, the monoterpene emissions were higher under warming than under normal temperature during the weeks 4, 6 and 7 (Fig. 1), but the low amount of replicates ($n = 2$–3) reduced the statistical power to detect differences. There were positive correlations between the number of *E. vaginatum* leaves and the emissions of monoterpenes and ORVOCs under warming, although the Pearson correlation coefficients were smaller than with isoprene. Thus, the increased number of *E. vaginatum* leaves under warming did not convert into higher monoterpene, sesquiterpene, ORVOC and other VOC emissions, as it did for isoprene. In general, woody plants are recognized as monoterpene and sesquiterpene emitters contrary to graminoids (Laothawornkitkul et al. 2009). It appears that the stress caused by water table drawdown was more important for the BVOC emissions than the warming effect in the time frame of this experiment.

In the peat samples, no isoprene was emitted, which is in line with previous BVOC measurements

from peat soils (Beckmann and Lloyd 2001; Tiiva et al. 2009). Furthermore, warming did not affect emissions of any other BVOCs from the peat, which follows the trend measured at the surface of the microcosms where warming did not affect emissions of BVOCs other than isoprene. In addition, the warming treatment was not applied during the actual peat samplings done separately at the end of the experiment.

Low BVOC emissions from the boreal peatland microcosms

The BVOC emissions from the unmanipulated boreal peatland microcosms were in the same order of magnitude as those measured in other growth chamber experiments (Electronic Supplementary Table S2; Tiiva et al. 2009; Faubert et al. 2010c). However, the isoprene and monoterpene emissions were lower than those measured from boreal peatlands and forests using chamber techniques in the field (Klinger et al. 1994; Janson et al. 1999). Klinger et al. (1994) measured isoprene and monoterpene emissions from boreal peatlands of the Hudson Bay lowland ranging between 0.8–104.2 mg C m^{-2} h^{-1} and 0–146.3 mg C m^{-2} h^{-1}, respectively. Janson et al. (1999) measured isoprene and monoterpene emissions from a boreal *Sphagnum* fen that were between 55–408 μg C m^{-2} h^{-1} and 19–90 μg C m^{-2} h^{-1}, respectively. Isoprene and monoterpene emissions measured from a bog forest were 0–9.6 mg C m^{-2} h^{-1} and 40–67.5 mg C m^{-2} h^{-1}, respectively (Klinger et al. 1994). In a black spruce forest, isoprene and monoterpene emissions ranged between 6.3–150.4 mg C m^{-2} h^{-1} and 192.9–293.3 mg C m^{-2} h^{-1}, respectively (Klinger et al. 1994). Factors such as differences in the measurement techniques, water conditions, vegetation composition, and temperature and light conditions during the measurements can be responsible for the different scales of BVOC emissions between studies.

In general, there can be some uncertainties in the emission rates measured by chamber methods such as the one used in this study. During the measurements, there can be uncertainties related to the increase in air humidity in the chamber headspace and air replacement/mixing ratio (Ortega and Helmig 2008). Despite these sources of errors, the chamber method used in this study was ideal and the most convenient for comparison of the treatment effects.

The relationship between BVOC emissions and CO_2 and CH_4 exchanges

Water table drawdown increased the oxic conditions in the microcosms, increasing CO_2 emission as a result of increased dark ecosystem respiration and decreased photosynthesis (Moore and Knowles 1989; Moore and Dalva 1993; Strack 2008). Moreover, oxic conditions in the microcosms with water table drawdown increased CH_4 oxidation most probably caused by an increased activity of methanotrophic bacteria (Moore and Knowles 1989; Sundh et al. 1994; Strack 2008). Warming increased dark ecosystem respiration and CH_4 emission most likely due to the increased enzymatic activity of the peat microbial community and methanogenic bacteria (Moore and Dalva 1993; Christensen et al. 2003; Lafleur et al. 2005; Strack 2008).

In the microcosms with natural water table, carbon emitted as BVOCs was less than 1% of the CO_2–C uptake. This proportion is in the same range as the one reported by Tiiva et al. (2009) for boreal peatland microcosms of hollow topography with natural water table. On a subarctic peatland in northern Finland, the carbon emitted as BVOCs was also in the same range as in the present experiment (Tiiva et al. 2007a; Faubert et al. 2010b). However, on a subarctic peatland in northern Sweden, Bäckstrand et al. (2008) report that the proportion of carbon emitted as BVOCs is as much as 5% of the CO_2–C uptake. In Mediterranean and tropical ecosystems, proportions of carbon emitted as BVOCs of the CO_2–C uptake vary between 0.07 and 12.4%, which is the same range or up to two orders of magnitude higher than in the present experiment (Kesselmeier et al. 2002; Kuhn et al. 2007). Carbon emitted as BVOCs can be up to 10% of the carbon uptake, or even more, under stressful conditions (Peñuelas and Llusià 2003). The carbon emitted as BVOCs was 1.5–3% of the carbon emitted as CH_4 in the microcosms with natural water table. This proportion is in the same magnitude as in another experiment conducted by Tiiva et al. (2009) and on a subarctic peatland in Northern Finland (Tiiva et al. 2007a; Faubert et al. 2010b).

Conclusion

Climate warming is expected to have a direct effect on the ecology and biogeochemistry of boreal peatlands. An indirect effect of climate warming is also expected with water table drawdown following an increased evapotranspiration. This experiment showed that the effect of water table drawdown surpassed the effect of warming by decreasing the emissions of all BVOC groups from boreal peatland microcosms. Warming only increased isoprene emission. Thus, our results suggest that indirect effect of climate warming on peatland ecosystems through the water table drawdown could alter the expected temperature-dependent increase of BVOC emissions.

The effect of water table drawdown on boreal peatland decreases the CH_4 emission, which is a negative radiative forcing on climate warming. On the other hand, water table drawdown increases the CO_2 emission to the atmosphere, which is a positive radiative forcing. Moreover, the reduction of the reactive BVOC emissions by water table drawdown may reinforce positive radiative forcing if the emission reduction decreases the cooling effect induced by the lower formation rate of secondary organic aerosols. These factors with concomitant negative and positive radiative forcings on climate warming should be considered in the modeling of the atmospheric chemistry in the boreal regions under climate warming.

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